25. On the Organ of Jacobson and its Relations in the "Insectivora."—Part II. *Talpa*, *Centetes*, and *Chrysochloris*. By Lieut. R. Broom, M.D., D.Sc., C.M.Z.S., R.A.M.C.

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When six weeks ago I undertook the examination of the Organ of Jacobson and its relations in *Tupaia* and *Gymnura*, I was merely anxious to see if *Tupaia* agreed with *Macroscelides*, and *Gymnura* with *Erinaceus*, as an agreement would give further evidence of the value of this region of the skull as a basis of classification, and also strongly support the removal of *Macroscelides*, *Tupaia*, and allied genera from the Insectivora and the placing of them in a distinct order—Menotyphla. As I have shown in Part I. of this paper, *Tupaia* agrees sufficiently closely with *Macroscelides*—both having the Polyprotodont Marsupial type of organ—to admit of their being placed in the same order; while *Gymnura* was shown to have the higher Eutherian type of organ met with in *Erinaceus*, *Felis*, *Ovis*, and all higher forms in which the organ is retained.

When I had finished the study of these two types, I thought it would be worth while to look at the condition in the aberrant African Golden Mole, *Chrysochloris*; and as Prof. J. P. Hill had two very fine specimens which I had given him some years ago—a newly-born *Chrysochloris hottentota* and a slightly older *Chrysochloris asiatica*—he very kindly had the heads sectioned so that I might examine them. The results were so interesting that it was necessary to go further with the research. Through the kindness of Mr. Oldfield Thomas, of the British Museum, I obtained the snout of a *Centetes* which I have examined, and also adult specimens of the common mole and shrew. Prof. Hill very kindly had sectioned for me the head of a very young mole. To these gentlemen, and also to Prof. Hill's laboratory assistant, Mr. F. Pittock, I am deeply indebted.

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[*] For explanation of the Plates see p. 354.

The Organ of Jacobson in Talpa. (Pl. III. figs. 1–7.)

Prof. Kitchen Parker in 1885 figured a number of sections of the nose of the young of *Talpa*. While these show the general structure and relations of the nasal cartilages, they do not clearly show the structures in the neighbourhood of the naso-palatine canal.

Though the young mole which I have examined has the cartilage in the anterior part of Jacobson's duct imperfectly chondrified, the young animal reveals the structures more clearly than does the adult in which the bones are so highly ossified and anchylosed.

In the anterior part of the nose there is little worthy of special note. One unusual feature is the thinning-out and perforation of the cartilage of the septum a short distance behind the plane of the nostril. As the sections of the snout have been cut of uniform thickness, the number of the section figured or described will indicate the situation of the various features. This anterior perforation of the septal cartilage is between sections 19 and 22.

Immediately behind the perforation the upper part of the septum begins to thicken. Fig. 1 represents section 36. The thick alinasal cartilage is seen curving round and united with the thick outer part of the anterior nasal-floor cartilage. Outside the cartilage is seen the lacrimal duct, and inside, the duct of the nasal gland.

From the plane of this last section to section 76, the nasal cavity is completely surrounded by cartilage. The upper part of the septal cartilage becomes gradually more thickened. From section 60 a median groove passes upwards into the lower part of the septum gradually dividing the cartilage into two. Fig. 2 represents section 74. Here the lower parts of the median cartilage are almost separated from the upper septal cartilage to form the recurrent cartilages. The anterior part of the premaxilla is seen; the bones of the two sides are not clearly separable.

Three or four sections beyond that shown in fig. 2 the recurrent cartilage is free from the base of the septum and also from the lower part of the alinasal. A similar condition occurs for about twenty sections. In section 96 is seen the anterior part of the naso-palatine canal.

Fig. 4 represents the condition at section 100. On the left side the duct of Jacobson's organ is seen opening into the canal. On the right side, the duct of the organ is seen lying above and slightly to the outer side of the canal. The anterior part of Jacobson's cartilage is seen lying above the duct. The recurrent cartilage is well developed.

Fig. 3 represents section 103. The duct of Jacobson's organ is seen immediately above the naso-palatine duct.

In fig. 5, which represents section 110, the naso-palatine duct is shown to be passing to the outer side of the Jacobson's duct, and Jacobson's cartilage coming to lie on the inner side of the duct. The palatine process of the premaxilla is seen on one side free from the premaxilla.

A few sections further back, as shown in fig. 7, which represents section 117, Jacobson's cartilage is united with the lower part of the recurrent cartilage, and the naso-palatine canal is seen to have opened into the nasal cavity. In the next four sections, veins are seen to pass through two fair-sized openings in the cartilage about the level of the upper part of the palatine process

In fig. 6 is represented section 126. Here the duct of Jacobson's organ is just about to open out into the organ proper. The palatine processes form flattened splints on the inner sides of the cartilages of Jacobson. A portion of the secondary palatal plate of the maxilla is seen in the section.

The organ of Jacobson as distinct from the duct extends from section 127 to section 178. The specimen examined is too young to show clearly the arrangement of blood-vessels in connection with the organ. Beyond section 178 the organ is continued into a glandular duct, which extends for ten more sections.

Talpa agrees with *Gymnura* in having feebly developed glandular ridges; in having practically no inferior turbinal in that part of the nose in which is situated the anterior part of Jacobson's organ; in having the lower half of the nasal septum converted into recurrent cartilages: and in Jacobson's organ having a long duct in front which opens into the anterior end of the naso-palatine canal. It differs in a number of details, such as the mode of opening of Jacobson's duct, the less forward extension of Jacobson's cartilage, in the arrangement of the blood-vessels of the organ, and in the better development of the recurrent cartilages.

There can, however, I think be little doubt but that *Talpa* is allied to *Gymnura* and may conveniently be left in the old order Insectivora.

I have made a series of sections of the snout of an adult *Sorex*. Unfortunately, the specimen was not in the best state of preservation, and, further, the structures are so extremely ossified that it is difficult to interpret some of the parts, and a young specimen will require to be examined before one can speak with any confidence on the affinities. In certain features *Sorex* resembles *Centetes* even more than it does *Talpa*, and an examination of the nose of a late fœtus would probably reveal some interesting facts.

The Organ of Jacobson in Centetes. (Pl. III. figs. 8–14.)

The specimen examined was the snout of an adult *Centetes ecaudatus* in fairly good preservation. It was sectioned by hand.

In the anterior part of the snout the median septum is well developed and of about uniform width. On passing back, the upper and middle part becomes thickened; then a little further back the lower half widens out and becomes divided by a median cleft into the two recurrent cartilages, as seen in fig. 8. Though in this section the alinasal is seen detached from the recurrent cartilage, they are seen united a few sections further forward. If this section be compared with a corresponding section in *Talpa*, such as shown in fig. 2, it will be observed that though there are many minor differences there is considerable agreement. Even the somewhat corresponding section which I have figured in *Gymnura* will be seen to agree fairly well, while the corresponding section in *Tupaia* will be seen to differ very greatly.

On passing a little further back, the septal cartilage becomes divided into an upper and a lower part. The upper part soon becomes greatly reduced, and then completely lost, while the lower part is continued backwards as a rounded cartilaginous rod. In fig. 9 the section passes through the anterior part of the papilla. The recurrent cartilages lie by the base of the septum. The upper nasal cartilages are considerably reduced.

Fig. 10 represents a section further back. It shows the anterior part of the naso-palatine canal. On the one side, Jacobson's duct is seen opening into it. At this plane the only cartilaginous support of the ducts is the anterior extension of the posterior nasal-floor cartilage. The recurrent cartilage is still of large size.

Fig. 11 represents a section near the plane where the naso-palatine canal opens into the nasal cavity. The recurrent cartilage is greatly reduced. Jacobson's duct is seen supported by anterior processes of Jacobson's cartilage.

Fig. 12 represents a section a short distance behind that shown in fig. 11. A small process of the recurrent cartilage is still seen, and quite free from Jacobson's cartilage. Jacobson's cartilage is united at its outer lower side to the posterior nasal-floor cartilage. This is a most unusual condition, and, so far as I am aware, is only known elsewhere in *Procavia*.

In fig. 13 Jacobson's organ and the cartilage are well developed. There is a small nasal-floor cartilage still seen. The palatine processes are large and partly roof over the organ. Above the palatine process is seen the anterior end of the vomer.

Fig. 14 is considerably further back. The vomer nearly clasps the nasal septum. Jacobson's cartilage rests on the palatal plate of the maxilla. The palatal processes, though thin, are still of large size. In this same section, though not shown in the figure, is seen a large inferior turbinal supported by a slender turbinal bone, and further up on the outer nasal wall a very well developed glandular ridge.

Centetes presents a number of unusual characters. It agrees with *Gymnura* and *Talpa* in that Jacobson's organ has a long narrow duct which opens into the anterior end of the naso-palatine canal, but differs from both in the anterior part of Jacobson's cartilage being less developed. It differs from both in the greater development anteriorly of the inferior turbinal. It resembles *Gymnura* in having a single large blood-vessel along the outer side of the organ. In the loss of the upper part of the septal cartilage, it agrees with *Sorex*. I know of no other form besides *Centetes* in which the lower part of the septal cartilage is completely surrounded by the vomer, as it is a little behind the plane of Jacobson's organ.

Whether *Centetes* should be placed with *Gymnura* and *Talpa* in the order Insectivora, or placed in a separate order of the Cœnorhinata, the evidence from the structures in the nose does not conclusively show, and it will therefore be well at present to leave *Centetes* and its allies in a very distinct family or suborder of the Insectivora.

The Organ of Jacobson in Chrysochloris. (Plate IV.)

I have examined the organ and its relations in a newly-born *Chrysochloris hottentota*, and a somewhat older *Chrysochloris asiatica*. The former had a head-length of 12 mm., and the latter a head-length of 16 mm.

Fig. 1 represents section 40 of the nose of the newly-born *Chrysochloris hottentota*. The median septum is slender; the alinasals are very wide. In the general arrangement of the cartilages, and in the mode of opening of the naso-lacrimal duct, the agreement with *Tupaia* is fairly close.

Fig. 2 represents section 47. It will be unnecessary in the present paper to discuss the morphology of the small cartilages of the nasal valve, but this section shows a remarkable recurrent process from the outer border of the alinasal. The only other mammal I know of which possesses a similar structure is *Echidna*.

In fig. 3, which represents section 55, the most anterior part of the premaxilla is cut through. The alinasal is continuous with the anterior nasal-floor cartilage, and a very sharp fold passes into the inferior turbinal.

Fig. 4 represents section 64. Here the lower part of the premaxilla is cut across as well as the lateral. The nasal-floor cartilage is no longer connected with the alinasal. The septal cartilage shows the first indications of separating into upper and lower parts.

In fig. 5, which represents section 69, we see the division of the septal cartilage into upper and lower parts, and the commencing division of the lower into the two recurrent cartilages. In this and the previous sections, the great encroachment on the nasal cavity by the folding of the mucous membrane is seen to be in marked contrast to the condition seen in *Talpa*, *Gymnura*, and *Centetes*.

Fig. 6, which represents section 86, cuts through the first incisors. The premaxillaries are sending up processes which form the bases of the palatine processes. The recurrent cartilages resemble considerably those of the Diprotodont Marsupials, *Trichosurus* and *Pseudochirus*.

In fig. 7, which represents section 114, is seen the anterior part of the maxilla. Here the recurrent cartilage is even more Diprotodont-like than in the previous section figured. The section is through the anterior part of the papilla.

Fig. 8, which represents section 120, is through the naso-palatine canal. It will be observed that the canal opens directly up into the nose, as in the typical marsupials. Jacobson's cartilages have given off the outer bars.

Fig. 9 represents section 123. Here Jacobson's organ is seen opening directly into the lower part of the nasal cavity. This section is strikingly like figures I have given of Jacobson's organ in *Pseudochirus* and *Trichosurus*.

In fig. 10, which represents section 126, the organ is seen in its fullest development.

A short distance behind this last section a small but well chondrified posterior nasal-floor cartilage is developed. The cartilage on passing backwards comes to lie underneath the outer part of Jacobson's cartilage.

Figs. 11–13 represent three sections through Jacobson's organ in the young *Chrysochloris asiatica*. Section 11 is through the anterior end of the organ near where it opens into the lower part of the nasal cavity: section 12 is through the middle of the organ, and section 13 near its posterior end. One of the most remarkable characters of the sections is the folding-down of the inferior turbinal till it almost forms a secondary nasal floor. The organ itself is remarkable in having no outer vascular plexus nor, as is seen in most Marsupials and in *Gymnura*, *Centetes*, and *Tupaia*, a large vessel along the outer side. Further, while the organ in most mammals has a large gland or numerous glands opening into it posteriorly, *Chrysochloris* has mucous glands opening into it all along its upper border.

It will be observed that *Chrysochloris* differs in the structure of this region of the nose entirely from *Gymnura*, *Talpa*, and *Centetes*, and that while it agrees more with *Tupaia* and *Macroscelides*, the affinity is not close.

Conclusions.

The research into the structure of the anterior nasal region of the Insectivores, even though only a few of the more striking types have been examined, shows I think conclusively that the "Insectivora" is not a natural order. *Erinaceus*, *Gymnura*, *Talpa*, *Sorex*, and *Centetes* agree in each having an organ of Jacobson which ends in a long duct opening into the naso-palatine canal near its anterior part. Jacobson's cartilage in each passes forwards with the duct, and the naso-palatine canal is supported by an anterior process of the posterior nasal-floor cartilage. Whatever subdivision may on other grounds be made of these Insectivores they all belong to the Cœnorhinata, and agree with most higher mammals, such as the Carnivores and Ungulates.

Tupaia and *Macroscelides* agree in having a Polyprotodont marsupial type of structure, and cannot have any near affinity with the typical Insectivores, and the order Menotyphla to which they belong must be removed far from the Insectivora and placed in quite a different phylum and not far from the early Marsupials.

Chrysochloris, which has generally been regarded as allied to *Centetes*, is seen to be in no way closely related to it. Like *Tupaia*, *Chrysochloris* belongs to the Archæorhinata, but it cannot belong to the order Menotyphla. The resemblance of its nasal structures to those of the Diprotodont marsupials is puzzling, and until further work is done on the development of *Chrysochloris*, one must hesitate in discussing its affinities further.

In 1883 Dobson *, in discussing the affinities of *Chrysochloris*, wrote as follows :—" The natural relations of the species of the family are with the Centetidæ, which they resemble in the form of their molar teeth, in the absence of an interorbital constriction, in the position of the testes, and in some important myological characters ; but they also present many most important differences . . . . such as the presence and peculiar development of the zygomatic arches, the presence of tympanic bullæ, and the very different form of the male generative organs, characters which, while indicating separation at a very remote period from the ancestral Centetidæ, do not ally them with any other family of recent Insectivora."

The peculiar structure of the molars has been the main character which has suggested an affinity with *Centetes*. But we find a similar type of teeth in the marsupial *Notoryctes*, and the similarity in the three genera is probably due to convergence, and does not indicate any affinity.

I hope shortly to undertake the study of the structure and development of the skull, and may be able to throw some further light on the affinities of *Chrysochloris*.

In the meantime I have no hesitation in removing it from the Insectivora, and placing it in a distinct order, for which the name Chrysochloridea, proposed by Dobson, may be retained.

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* A Monograph of the Insectivora, Systematic and Anatomical, Part II., 1883, p. 108.

EXPLANATION OF THE PLATES.

Lettering.

a.J.c., anterior process of Jacobson's cartilage; *b.v.*, blood-vessel; *d.J.o.*, duct of Jacobson's organ; *g.d.J.o.*, duct of gland leading into Jacobson's organ; *J.c.*, Jacobson's cartilage; *J.o.*, Jacobson's organ; *l.d.*, lacrimal duct; *Mx.*, maxilla; *Na.*, nasal; *n.f.c.*, nasal-floor cartilage; *n.g.d.*, nasal-gland duct; *n.p.c.*, naso-palatine canal; *o.b.J.c.*, outer bar of Jacobson's cartilage; *Pmx.*, premaxilla; *p.Pmx.*, palatine process of premaxilla; *r.a.n.*, recurrent process of alinasal; *r.c.*, recurrent cartilage; *Vo.*, vomer.

PLATE III.

Figs. 1–4. Sections through the snout of *Talpa europæa*. Young. × 15.
5–7. Sections through the snout of *Talpa europæa*. Young. Showing Jacobson's duct. × 34.
8–9. Sections through the snout of *Centetes ecaudatus*. × 5.
10–14. Sections through the snout of *Centetes ecaudatus*. Showing Jacobson's organ and its duct, and their relations. × 10.

PLATE IV.

Figs. 1–7. Sections through the snout of a newly-born *Chrysochloris hottentota* (greatest length 28 mm.). Figs. 1–4, × 15. Figs. 5–7, × 20.
8–10. Sections through the papillary region of newly-born *Chrysochloris hottentota*, showing the mode of opening of Jacobson's organ. × 30.
11–13. Sections through the snout of young *Chrysochloris asiatica*. (About half-grown.) × 17.